Host Range Differences Between Populations of *Puccinia graminis* subsp. *graminicola* Obtained from Perennial Ryegrass and Tall Fescue

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ABSTRACT

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In the Pacific Northwest region of the United States, cool-season grasses grown for seed can be severely damaged by *Puccinia graminis* subsp. *graminicola*, causal agent of stem rust. Urediniospores of the pathogen, collected either from perennial ryegrass (*Lolium perenne*) or tall fescue (*Festuca arundinacea*), were tested for host range among selected grasses and cereals. Under greenhouse conditions, the inoculum from *L. perenne* could produce pustules on this host, as well as on *Dactylis glomerata*, *Lolium multiflorum*, *Poa pratensis*, and *F. rubra* subsp. *rubra* and subsp. *commutata*; it caused only limited pustule development (low incidence or pustule type) on *F. arundinacea*, *F. ovina* subsp. *hirtula*, *P. annua*, *Hordeum vulgare*, and *Secale cereale*. No symptoms were produced on *Triticum aestivum* or *Avena sativa*. The inoculum from *F. arundinacea* had a host range that included itself, *D. glomerata*, *L. perenne*, *L. multiflorum*, and *F. rubra* subsp. *rubra* and subsp. *commutata*; there was no sign of pustule development on *Poa* spp. or the cereal grains tested (*T. aestivum*, *A. sativa*, *S. cereale*, and *H. vulgare*). The two urediniospore populations differed also in rate of symptom development on most of their common hosts. There was a small, but statistically significant, difference in spore size among the populations from different hosts. No recommendation is made for separate taxonomic status of populations from *F. arundinacea* and *L. perenne*, but the adaptation of each to its own host should be considered when devising disease management strategies and studying host genetic resistance.

Additional keywords: forma specialis, stem rust

Cool-season grasses are intensively cultivated for seed production in western Oregon, where stem rust is the most damaging disease on several species, including perennial ryegrass (*Lolium perenne*), annual ryegrass (*L. multiflorum*), and tall fescue (*Festuca arundinacea*). Stem rust also occurs on seed crops of orchard grass (*Dactylis glomerata*) and red fescue (*F. rubra*) in the region.

The causal agent of stem rust in grasses and cereals is *Puccinia graminis* Pers.:Pers. Within this species, there exist distinct populations that differ in morphology (13) or in the host species they can infect (1). There has not been a uniform approach to nomenclature or taxonomy of these subspecific groups, a situation which also has been noted for the crown rust pathogen (6) and other rusts affecting cereals and grasses (14). Schwartz (14) notes that some taxonomists use a narrow host-based concept for delimiting rust species and subspecific groups, whereas others use a broader concept based principally on morphology. The existence of subspecific groups of the stem rust pathogen based on host range was first documented by Erickson (5), who called them formae speciales. Each forma specialis, although not restricted to a single host species or genus, has a unique constellation of compatible hosts. The first observation of a forma specialis in *P. graminis* from *Lolium* spp. was a 1948 report by Guyot et al. in France (8). In 1951, Waterhouse (17) described an Australian population of *P. graminis* pathogenic to *L. perenne* and 30 other grass species (including *F. arundinacea*, *D. glomerata,* and *Poa annua)* but not to species in genus *Avena*, *Triticum,* or *Secale*. He considered its spore morphology sufficiently distinct to designate it a subspecies, *P. graminis* f. sp. *lolii*. Shortly thereafter, a brief note by Guyot (7) reported inoculation studies in which his inoculum of *P. graminis* f. sp. *lolii* displayed a host range similar to that of the Australian population. Guyot (7) also reported a host range for *P. graminis* f. sp. *festucae* that included *F. arundinacea*, *F. ovina,* and *F. pratensis*; this form could not infect *L. perenne*, oat (*Avena sativa),* or rye (*Secale cereale*) and produced only small, poorly sporulating pustules (termed "low-infection type" in the rust literature; 11) on *D. glomerata*. Tajimi (15) conducted a study with *P. graminis* f. sp. *lolii* in Japan and found that this population had a host range that was generally similar to the French and Australian populations, but that included *A. sativa* as well as a fully susceptible reaction ("high-infection type") on *S. cereale* and *Phleum pratense*.

Urban (16), in a 1967 paper, divided *Puccinia graminis* into two subspecies, *P. graminis* subsp. *graminis* and *P. graminis* subsp. *graminicola*, based principally on spore morphology. He placed the *lolii* populations of Waterhouse (17) and Guyot (7) in *P. graminis* subsp. *graminicola*. In a comprehensive treatment of rust fungi on grasses and cereals, Cummins (4) follows Urban in using only morphological characters, thus placing various formae speciales (designated by other authors) into each of the morphological subspecies. Two studies have examined the host range of populations identified as *P. graminis* subsp. *graminicola* from grasses. A population from *Phleum pratense* in Eastern Europe was pathogenic to *D. glomerata*, *Poa pratense,* and *P. annua* (among many others) but did not cause symptoms on *L. perenne* or *F. arundinacea* (3). In Oregon, a population of *Puccinia graminis* subsp. *graminicola* collected from *F. rubra* subsp. *commutata* was found to be essentially nonpathogenic to *L. perenne* or *F. arundinacea* (19).

The host range of *P. graminis* subsp. *graminicola* populations from *L. perenne* or *F. arundinacea* in Oregon has not been evaluated. For optimum progress in research on resistance breeding and epidemic management, it is important to know whether the rust pathogen affecting *F. arundinacea* is the same as that affecting *L. perenne*, and whether the population or populations can cause disease symptoms on other grass seed crops in the region as well. The objective of this study was to test isolates of *P. graminis* subsp. *graminicola* from *L. perenne* and *F. arundinacea* for differences in ability to cause disease on a range of grass species.

MATERIALS AND METHODS

Inoculum of *P. graminis* subsp. *graminicola*. Urediniospores were obtained from multiple-cultivar field plantings in 2 years at each of two locations near Corvallis, OR. The spores were collected by means of a cyclone sampler (11)

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attached to the vacuum end of a gasoline-powered leaf blower. Separate collections were made from *F. arundinacea* and *L. perenne*; spores were dried overnight at 30% relative humidity, then stored at –60°C until used. The collections from the locations and years for each host species were mixed to make one population for each host. To eliminate the possibility that a population used for experimental inoculations could contain contaminating spores from the other host, each population was passed sequentially through two increases on the appropriate host under controlled conditions in a greenhouse. For these increases, the highly susceptible cvs. Bonanza (*F. arundinacea*) and Morningstar (*L. perenne*) were used, and inoculated plants were maintained in glass enclosures supplied with filtered air (0.45 µm) to prevent passage of contaminating rust spores. Spores from open pustules were collected into gelatin capsules fitted on a small vacuum spore sampler (fabricated by the University of Minnesota Biological Science Department, St. Paul) in a laminar-flow transfer hood. The collected urediniospores were dried at 30% relative humidity and stored at –60°C. Immediately before use, spore dormancy was broken by placing the spores, sealed in a watertight container, into a 43°C water bath for 1.5 min (11).

Host plants. Seed of cool-season grass crop species, certified by the Oregon State University Seed Certification Service for purity, was obtained from breeders or seed companies. The following cultivars were chosen because they are commonly grown in the region or have a known susceptibility to rust diseases: *L. perenne* cvs. Palmer, Morningstar, Loretta Nova, and Linn; *L. multiflorum* cvs. Marshall and Gulf; *F. arundinacea* cvs. Bonanza, Fawn, and Shenandoah; creeping red fescue (*F. rubra* subsp. *rubra*) cv. Jasper; Chewings fescue (*F. rubra* subsp. *commutata*) cvs. Shadow and SR5100; sheeps fescue (*F. ovina* subsp. *hirtula*) cv. Bighorn; hard fescue (*F. brevipila*) cvs. Nordic, Osprey, and SR3100; *D. glomerata* cvs. Benchmark and Potomac; and Kentucky bluegrass (*Poa pratensis*) cvs. Baron and Geronimo. Seed of annual blue grass (*P. annua*), a common weed in the region, was collected locally. Seed of cereal grains was obtained from the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) Cereal Disease Laboratory, which provided cultivars known to be fully susceptible to the stem rust forma specialis adapted to that host: *A. sativa* cv. Marvelous, barley (*Hordeum vulgare*) cv. Hiproly, *S. cereale* cv. Prolific, and wheat (*Triticum aestivum)* cvs. Line E and McNair.

Grasses were grown from seed in a greenhouse supplemented with artificial light (high-pressure sodium lamps, 430 W; Philips Lighting, Somerset, NJ) to provide 14-h day length, and maintained at day and night temperatures of 21 and 13°C, respectively, until time of inoculation. Plants were grown in vermiculite in pots ("Cone-Tainers", 3.8 by 24 cm; Ray Leach Co., Corvallis, OR), one plant per pot. They were watered daily, and fertilized every 2 weeks with 17 mg each of N, P_2O_5, and K_2O in 25 ml of water. Plants were 3 to 4 months old when inoculated. Cereal grain plants were started from seed, grown under the same conditions as grasses except that fertilizer was applied at 5 days after sowing, and inoculated at 7 days of age (11).

Inoculation. For each of the two urediniospore populations, a suspension of 90 mg of spores in 7.6 ml of Soltrol (a light mineral oil; 12) was prepared, resulting in a concentration of 5×10^6 spores/ml. Viability of spores was 80 ± 5% as determined by observation of germinating spores incubated on water agar plates overnight. Potted host plants were placed in random order in an inoculation chamber and sprayed with 1 ml of suspension per 50 plants. Air in the chamber was scrubbed with water spray between inoculations to remove residual spores from the air. After allowing the oil to evaporate from the leaves for 1 h, plants were placed in a large, plastic-lined enclosure where intermittent mist from a humidifier (1 h on, 2 h off) produced a layer of fine water droplets on the leaves. Plants were incubated in the dark at 18 ± 2°C overnight (15 h), then in the natural greenhouse light for 4 h as the temperature increased to 25°C and the leaf surfaces dried. Plants were then removed from the enclosure and placed on a greenhouse bench, with 14-h days (natural light supplemented with artificial light), and daily minimum and maximum temperatures of

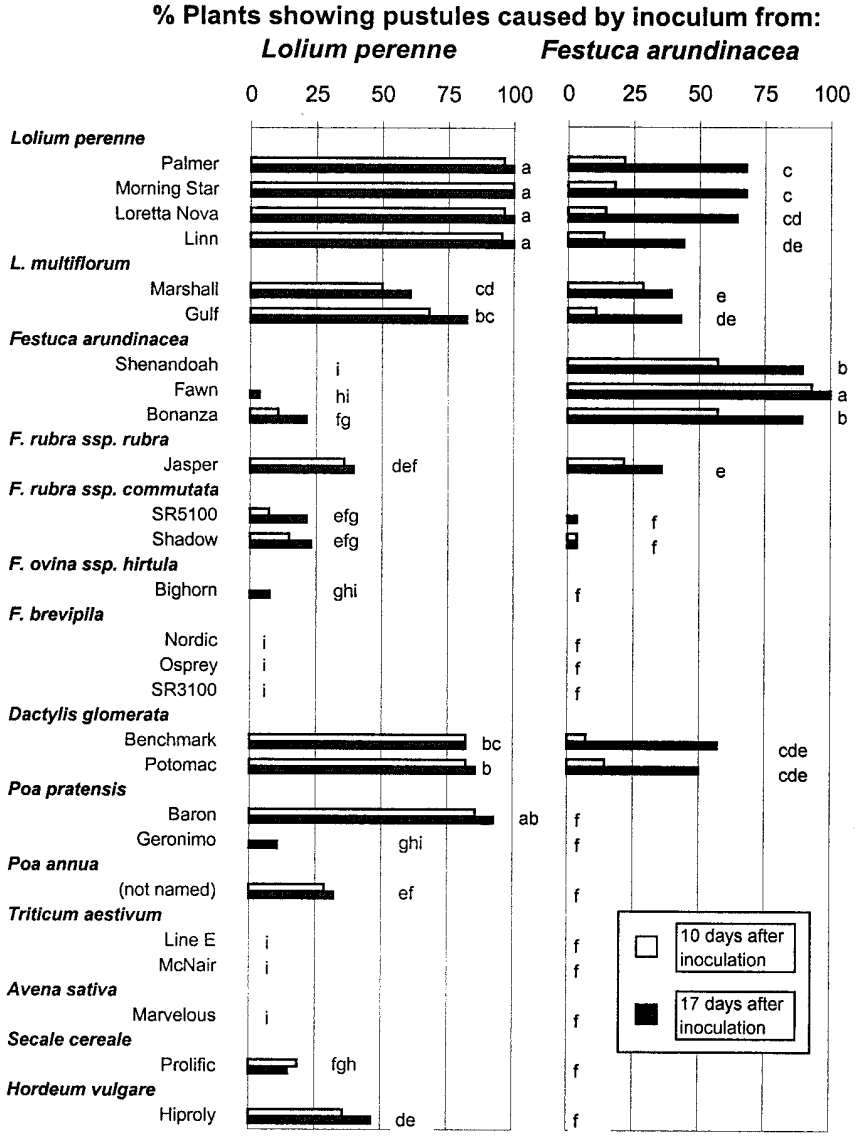

Fig. 1. Incidence of stem rust (% plants showing pustules) on indicated cultivars of grass species inoculated with urediniospores of *Puccinia graminis* subsp. *graminicola* that had been produced on either *Lolium perenne* or *Festuca arundinacea*. Incidence was assessed at 10 and 17 days after inoculation. Within an inoculum treatment, 17-day incidence bars with the same letter to the right are not significantly different ($P < 0.05$) as determined by Duncan's new multiple range test.

13 ± 2 and 23 ± 2°C, respectively. The experiment was conducted as a completely randomized design, with 14 replicates (pots) of each cultivar (grass or cereal) inoculated with each urediniospore population. This experiment was conducted twice to produce two trials for analysis.

Disease assessment. Plants were examined and disease assessments were made at 10 and 17 days after inoculation. The incidence (proportion of infected plants showing symptoms) and severity (number of open pustules on each infected plant) was recorded. Pustule types were scored on the following scale (11): 0 = no visible symptoms, ; = necrotic flecks, 1 = very small pustules with limited sporulation surrounded by necrosis or chlorosis, 2 = medium-size pustules with chlorosis, 3 = large pustules with abundant sporulation and marked chlorosis, and 4 = large pustules with abundant sporulation and little or no chlorosis. Pustules of type ; and 1 are generally referred to as low-infection type and pustules of type 3 and 4 are called high-infection type (11).

Urediniospore sizes. Urediniospores from each population were mounted in lactophenol (13) and examined at magnification ×640. Widths (at the widest part) and lengths of 50 spores were measured.

Data analysis. Incidence was transformed to arcsin(square root) before analysis by analysis of variance (ANOVA) using SAS (SAS System for Windows, release 6.11; SAS Institute, Cary, NC). Data for number of pustules per infected plant was non-normal in distribution, but approximately normal after values were transformed by taking logarithms of the data. ANOVA was performed on log-transformed data, using SAS. Separate analyses were done on the data from 10- and 17-day disease reading times. For each reading time, data from the two trials (i.e., the first experiment and the repeat) were combined and analyzed as a split-plot design with trial as the main plot. Trial was not statistically significant, and data presented in the figure and tables are means of the two trials. Mean separation was by Duncan's new multiple range test. Spore sizes were compared by a nonparametric *t* test, using SigmaStat (SigmaStat version 2.0; SPSS Inc., Chicago).

RESULTS

Host range of *Puccinia graminis* subsp. *graminicola* from *L. perenne*. Inoculum of the stem rust pathogen obtained from *L. perenne* produced pustules on all plants of the four *L. perenne* cultivars tested (Fig. 1). Based on data collected 17 days after inoculation, the incidence on this host of origin was significantly greater than the incidence on any other species tested, except for one cultivar of *Poa pratensis*. More than 50% of the plants of *L. multiflorum* and *D. glomerata* exhibited pustules at 17 days after inoculation with these urediniospores. Although the incidences on these hosts were significantly less than that on *L. perenne*, the pustules that occurred were of compatible (fully susceptible) type (Table 1). Furthermore, among the individual *L. multiflorum* and *D. glomerata* plants that were infected, the average severity (number of pustules per infected plant) was usually the same as that on *L. perenne* (Table 1). Incidence was approximately 30% on *F. rubra* subsp. *rubra* and *F. rubra* subsp. *commutata* (Fig. 1), significantly less than incidences on *L. perenne* or *D. glomerata*, but pustules were of compatible type (Table 1). Incidence on *P. annua* was over 25%, but infections produced only necrotic flecks or very small pustules. Very few plants of *F. ovina* subsp. *hirtula* exhibited pustules, and there were no symptoms of any kind among three cultivars of *F. brevipila*. In *F. arundinacea*, inoculum from *L. perenne* caused no compatible infections on cv. Shenandoah, very few on cv. Fawn, and less than 25% incidence on cv. Bonanza (Fig. 1). Pustule type on *F. arundinacea* ranged from ; to type 2, but most were type 1. On the cereal grains tested, inoculum from *L. perenne* was unable to produce pustules on *T. aestivum* or *A. sativa*, and produced a small number of necrotic flecks on less than 20% of the *S. cereale* plants. On *H. vulgare,* incidence was almost 50% (Fig. 1) and the number of pustules per infected plant was relatively large (Table 1), but pustules were very small and erupted only in chlorotic areas on the oldest leaves.

Host range of *Puccinia graminis* subsp. *graminicola* from *F. arundinacea*. Urediniospores of the pathogen obtained from *F. arundinacea* produced pustules on more than 80% of the plants of each cultivar of *F. arundinacea* that were tested (Fig.

Table 1. Characteristics of infection by *Puccinia graminis* subsp. *graminicola* on plants compatible to inoculum obtained from *L. perenne*

Species and cultivar	Severity[v]	Pustule type[w]
Lolium perenne		
Morning Star	2.32 a	3 (2–4)[x]
Palmer	1.95 ab	3 (2–4)
Linn	1.70 abc	3 (2–4)
Loretta Nova	1.48 bcd	2 (1–3)
Dactylis glomerata		
Benchmark	1.89 ab	2 (;–3)
Potomac	1.68 abc	2 (;–3)
L. multiflorum		
Gulf	1.54 abc	3 (1–3)
Marshall	1.32 bcde	3 (1–3)
Festuca rubra subsp. *rubra*		
Jasper	1.23 bcde	3 (1–4)
Hordeum vulgare		
Hiproly	1.20 bcde[y]	1 (;–2)
Poa pratensis		
Baron	1.20 bcde	2 (;–3)
Geronimo	0.23 fg	1 (;–1)
P. annua		
not named	0.63 efg	; (;–1)
F. ovina subsp. *hirtula*		
Bighorn	0.89 cdef	2 (2–4)
F. rubra subsp. *commutata*		
SR5100	0.64 efg	3 (2–4)
Shadow	0.63 efg	3 (;–4)
F. arundinacea		
Bonanza	0.71 defg	1 (;–2)
Fawn	0.10 g	1
Shenandoah[z]	0	;
F. brevipila		
Nordic	0	0
Osprey	0	0
SR3100	0	0
Secale cereale		
Prolific	0.12 g	; (;–1)
Triticum aestivum		
Line E	0	0
McNair	0	0
Avena sativa		
Marvelous	0	0

[v] Average of log (number of pustules per diseased plant). Plants not showing symptoms were not included in calculations.
[w] Pustule types: 0 = no visible symptoms of infection, ; = necrotic fleck, 1 = very small pustule with chlorosis and little sporulation, 2 = medium-size, with chlorosis, 3 = large, abundant sporulation, chlorosis, 4 = large, abundant sporulation, little or no chlorosis.
[x] Most frequent pustule type (range of types in parentheses).
[y] Pustules only on oldest leaves and in area of extensive chlorosis.
[z] Small number of plants with necrotic flecks.

1). Incidence was greater than 50% in both cultivars of *D. glomerata* and in three of the four *L. perenne* cultivars in the test. More than 25% of the *L. multiflorum* and *F. rubra* subsp. *rubra* plants exhibited pustules, but few plants of *F. rubra* subsp. *commutata* did. Pustules on these hosts were predominantly of compatible type, although necrotic flecks were not uncommon on *D. glomerata* and *L. perenne* (Table 2). Among individual plants susceptible to infection by this inoculum, severity on *F. arundinacea* was the same as that on *D. glomerata*, *L. perenne,* and *F. rubra* subsp. *rubra*, but was greater than severity on susceptible plants of *L. multiflorum* or *F. rubra* subsp. *commutata* (Table 2). A small number of plants of one *F. brevipila* cultivar had necrotic flecks, but otherwise there was no visible indication of infection on species of *Poa* or on *F. ovina* or *F. brevipila*. This inoculum was unable to cause disease on *T. aestivum*, *S. cereale,* or *A. sativa*, and on *H. vulgare* it caused only necrotic flecks on a small number of plants.

Table 2. Characteristics of infection by *Puccinia graminis* subsp. *graminicola* on plants compatible to inoculum obtained from *Festuca arundinacea*

Species and cultivar	Severity[w]	Pustule type[x]
Festuca arundinacea		
Fawn	1.86 a	3 (1–4)[y]
Bonanza	1.82 a	3 (1–4)
Shenandoah	1.76 a	3 (1–4)
Dactylis glomerata		
Potomac	1.57 ab	2 (;–3)
Benchmark	1.34 abc	1 (;–3)
Lolium perenne		
Linn	1.25 abc	2 (;–3)
Morning Star	1.23 abc	2 (;–4)
Loretta Nova	1.09 abc	2 (;–3)
Palmer	1.08 abc	2 (;–3)
F. rubra subsp. *rubra*		
Jasper	1.08 abc	2 (2–3)
L. multiflorum		
Marshall	0.92 bc	2 (1–4)
Gulf	0.85 bc	2 (1–3)
F. rubra subsp. *commutata*		
Shadow	0.78 c	3 (1–4)
SR5100	0.68 c	3
F. ovina subsp. *hirtula*		
Bighorn	0	0
F. brevipila		
Nordic	0	0
Osprey	0	0
SR3100	0	0
Poa pratensis		
Baron	0	0
Geronimo[z]	0	;
P. annua		
non-named	0	0
Hordeum vulgare		
Hiproly[z]	0	;
Secale cereale		
Prolific	0	0
Triticum aestivum		
Line E	0	0
McNair	0	0
Avena sativa		
Marvelous	0	0

[w] Average of log (number of pustules per diseased plant). Plants not showing symptoms are not included in calculations.

[x] Pustule types: 0 = no visible symptoms of infection, ; = necrotic fleck, 1 = very small pustule with chlorosis and little sporulation, 2 = medium-size, with chlorosis, 3 = large, abundant sporulation, chlorosis, 4 = large, abundant sporulation, little or no chlorosis.

[y] Most frequent pustule type (range of types in parentheses).

[z] One to two plants with necrotic flecks.

Table 3. Sizes of stem rust urediniospores in populations obtained from *Lolium perenne* and *Festuca arundinacea*[y]

	Source of urediniospores	
Dimension[z]	*L. perenne*	*F. arundinacea*
Length (µm)		
Mean	25.5	27.8
Standard deviation	2.3	2.4
Range	(19.8) 21.3–28.9 (30.4)	(22) 24.3–31.9 (33.4)
Mode	25.8	28.9
Width (µm)		
Mean	15.8	17.6
Standard deviation	1.2	1.1
Range	(13.7) 14.4–18.2 (18.2)	(15.2) 16–19.8 (19.8)
Mode	15.2	18.2

[y] Measured 50 spores of each population.

[z] Mean: *L. perenne* and *F. arundinacea* inoculum sources differ ($P < 0.01$) from each other for mean length and width. Range: 90% of spores are within the specified size range, and extreme values observed are shown in parentheses.

Pustule development rate. Incidence of disease caused by inoculum from *L. perenne* was not significantly greater at 17 days after inoculation than at 10 days postinoculation (Fig. 1, *analysis not shown*) for all species except *F. ovina* subsp. *hirtula*. In contrast, incidence of disease caused by inoculum from *F. arundinacea* was less at 10 days than at 17 days for several host species (*F. arundinacea*, *L. perenne*, *D. glomerata*, and *F. rubra* subsp. *rubra;* Fig. 1). That is, in most cases, pustule development was slower for hosts infected by the *F. arundinacea* population of *Puccinia graminis* subsp. *graminicola* than for the same hosts infected by the *L. perenne* population of the pathogen.

Urediniospores sizes. Spore sizes for both inoculum types were within the reported range (4) for *P. graminis* subsp. *graminicola* (Table 3) and most had three or four equatorial germination pores. There was a slight difference between the populations in urediniospore size. Mean spore length and width were significantly ($P < 0.01$) greater in the population from *F. arundinacea* than in that from *L. perenne*, although the ranges overlapped.

DISCUSSION

Results of these experiments demonstrate that there is genetic variability within *P. graminis* subsp. *graminicola* in western Oregon, evidenced by differences in host range. The inoculum obtained from *L. perenne* had a different, and wider, host range than inoculum obtained from *F. arundinacea*. In each case, inoculum consisted of the population that had been collected from diverse, field-grown cultivars at two locations and in 2 years, so each inoculum may include a diversity of genotypes adapted to the particular host species. Further study, however, will be required to determine whether the populations used are representative of populations on these two grasses throughout the region, and whether other identifiable subgroups of the pathogen occur on one or both hosts. Nonetheless, it is clear that there are subgroups that differ in important ways within the morphological subspecies.

The most important difference between the populations from *F. arundinacea* and *L. perenne* is in host range, and in reaction type, incidence, and severity on susceptible hosts. By these criteria, the population from *F. arundinacea* was best adapted to its host of origin and to several additional species, namely *L. perenne*, *L. multiflorum*, *D. glomerata,* and *F. rubra* (Fig. 1, Table 2). It caused no symptoms of any type on *Poa* spp. or on any cereal grains tested. In contrast, the population of *Puccinia graminis* subsp. *graminicola* from *L. perenne* is highly adapted to this host and to one of the two cultivars of *Poa pratensis* tested (Fig. 1, Table 1). It is also well adapted to *L. multiflorum* and *D. glomerata* and to a significant proportion of plants in *F. rubra*. It is not well adapted to *F. arundinacea*, although it is able to form visible infections (mostly of pustule type ; or 1) at a low incidence on some cultivars. It can form pustule types ; or 1 on *S. cereale* and *H. vulgare* under greenhouse conditions. The host range of rust pathogens in nature is generally narrower than that determined in greenhouse inoculations (1), and it is unlikely that *S. cereale*, *H. vulgare*, *Poa annua*, or *F. ovina* subsp. *hirtula* can support a *Puccinia graminis* subsp. *graminicola* population of the *L. perenne* type in nature. However, the fact that it can infect these hosts when inoculated distinguishes it clearly from the *F. arundinacea* population of *P. graminis* subsp. *graminicola*, which was unable to cause any visible infection on identical host cultivars under identical conditions. Further, it appears unlikely that the population from *L. perenne* could be supported on *F. arundinacea* in nature.

In addition to host range, these populations differed in other characteristics. The population from *L. perenne* has slightly smaller urediniospores than the population from *F. arundinacea*. Also, the population from *F. arundinacea* had a slower rate of pustule development than the *L. perenne* population of the pathogen on most of their common hosts. That is, the latent period (time between infection initiation and the production of new inoculum from the infection) is longer for the population from *F. arundinacea*. This is an epidemiologically significant factor, because latent period duration is of critical importance in competitiveness and epidemic rates for polycyclic pathogens.

Comparison of the host ranges for these populations with those of previously described *P. graminis* from grasses is complicated by the fact that infection conditions and host cultivars may differ among studies. In this study, an attempt was made to use the most susceptible host genotypes available, if known. Cultivars of *Lolium* spp., *F. arundinacea*, *D. glomerata,* and *F. brevipila* were considered by local grass-seed breeders and growers to be most susceptible to rust diseases; cultivars of other species were chosen from commonly grown cultivars. The cereal grain cultivars were supplied by the USDA Cereal Rust Laboratory as universal suscepts for stem rust. Therefore, it seems likely that absence of pustule development on these plant genotypes indicates lack of susceptibility in the species, but this is not certain. Most previous studies with grass stem rust (except that by Welty and Azevedo; 19) used different cultivars than were used in this research, or did not indicate the cultivars used. Despite these differences, and differences due to varying infection conditions, some comparisons can be made (Table 4). The population of *P. graminis* subsp. *graminicola* from *L. perenne* in this study has a host range among grasses similar to the Japanese, Australian, and French populations from *L. multiflorum* and *L. perenne*, except that the latter three produced susceptible type pustules (types 3 and 4) on a substantial proportion of *F. arundinacea* plants. There are also some differences with regard to infection of cereals: the population in the present study caused only low pustule types (type ; or 1) on barley and rye, whereas the French population produced type 3 and 4 pustules on barley, and the Japanese population caused the same type of pustules on barley, rye, and some oat cultivars. These populations differed markedly in host range from the *P. graminis* subsp. *graminicola* obtained from *Phleum pratense* in Czechoslovakia (3) as well as the isolate from *F. rubra* in Oregon (19), both of which are unable to produce pustules on *F. arundinacea* or *L. perenne* at a significant level. The population from *F. arundinacea* in this study appears to differ from the one described by Guyot (7), in that the latter was unable to produce large, type 3 and 4 pustules on *L. perenne*. As noted by Anikster (1) and Urban (16), a forma specialis in a particular geographic area is the product of host–pathogen relationships that occur there over time, so the host ranges of physiological forms that are mostly similar may yet be somewhat different from one region to another.

The form of *Puccinia graminis* subsp. *graminicola* from *F. arundinacea* is clearly different than the one from *L. perenne*, but may have arisen from it. Stem rust was well-established on *L. perenne* in the Pacific Northwest (10) for more than a decade before it first appeared on *F. arundinacea* in the region (18). It is postulated (2) that new formae speciales of *Puccinia* spp.

Table 4. Comparison of published host ranges for stem rust isolates from genus *Lolium* and *Festuca*

	Inoculum source[u]					
Inoculated host	***L. perenne* (Australia)[v]**	***L. perenne* (France)[w]**	***L. multiflorum* (Japan)[x]**	***L. perenne* (USA)[y]**	***F. arundinacea* (USA)[y]**	***F. rubra* (USA)[z]**
L. perenne	+	+	+ (95)	+ (100)	+ (60)	0/[+] (<5)
L. multiflorum	+	+	+ (90)	+ (70)	+ (40)	nt
Dactylis glomerata	+	+	+ (80)	+ (85)	+ (55)	nt
Poa pratensis	nt	nt	+/0 (0–70)	+/[+] (10–90)	0/[+] (<5)	nt
P. annua	+/0	nt	[+] (30)	[+] (30)	0	nt
F. arundinacea	+	+	+ (15)	[+] (0–20)	+ (90)	0
F. rubra	nt	nt	+ (40)	+ (30)	+ (5–35)	+ (80)
F. ovina	nt	nt	+ (100)	+ (7)	0	+ (10)
F. brevipila	nt	nt	Nt	0	0	nt
Hordeum vulgare	[+]	+	+ (100)	[+] (45)	0/[+] (<5)	nt
Secale cereale	0	0	+ (95)	[+] (15)	0	nt
Avena sativa	0/[+]	0	+ (0–100)	0	0	nt
Triticum aestivum	0	0	0	0	0	nt

[u] + = Inoculum produced susceptible pustule type in greenhouse test or was isolated from natural infections; [+] = produced low pustule type (flecks or very restricted pustules) or low incidence in greenhouse inoculations; 0 = produced no observable symptoms; nt = not tested for this host–pathogen combination; numbers separated by / indicate-different reaction types observed on different cultivars of the same species; and numbers in parentheses = percent plants diseased in greenhouse tests, for those reports with such data.

[v] Waterhouse (1951). Partial listing.

[w] Guyot (1961). Partial listing.

[x] Tajimi (1975). Partial listing.

[y] Pfender (this report).

[z] Welty and Azevedo (1995).

have arisen through gene recombination that resulted in increased virulence on certain hosts at the expense of virulence on others. The alternate host for *P. graminis* is not known to exist in western Oregon; therefore, sexual recombination is unlikely. However, Luig and Watson (9) documented the occurrence of natural somatic hybridization in *P. graminis*, and this could be a source of novel genotypes of the pathogen on grasses. A novel type with increased fitness on *F. arundinacea*, but reduced fitness on other grasses (in terms of latent period and host range), could have arisen from the *P. graminis* subsp. *graminicola* population adapted to *L. perenne*.

The primary conclusion of this study, that there are subgroups of *P. graminis* subsp. *graminicola* differentially adapted to *L. perenne* and *F. arundinacea* in Oregon, is important for research and implementation of disease management in these crops. In testing for host genetic resistance, the appropriate population of the pathogen must be used. Disease management approaches that are related to sources of inoculum should also be based on a knowledge of the existence and host ranges of pathogen populations adapted to the different hosts.

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